University of Kansas Publications
Museum of Natural History

Volume 17, No. 11, pp. 503-515, 5 figs.
March 20, 1968

Genera of Leptodactylid Frogs in México

BY

JOHN D. LYNCH

University of Kansas
Lawrence
1968

University of Kansas Publications, Museum of Natural History
Editors: E. Raymond Hall, Chairman, Henry S. Fitch,
Frank B. Cross

Volume 17, No. 11, pp. 503-515, 5 figs.
Published March 20, 1968

University of Kansas
Lawrence, Kansas

PRINTED BY
ROBERT R. (BOB) SANDERS, STATE PRINTER
TOPEKA, KANSAS
1968
31-9418

Genera of Leptodactylid Frogs in México

BY JOHN D. LYNCH

INTRODUCTION

According to the most recent review of the Mexican amphibian fauna (Smith and Taylor, 1948), six genera of leptodactylid frogs occur in México. One other genus, *Pleurodema,* occurs in Lower Central America. Smith and Taylor recognized one species of *Engystomops,* 28 of *Eleutherodactylus,* three of *Leptodactylus,* eight of *Microbatrachylus,* 12 of *Syrrhophus,* and five of *Tomodactylus.* Subsequent to the publication of their checklist of the Mexican amphibia (1948), numerous taxonomic changes have been proposed. Many species of *Eleutherodactylus* have been added to the fauna, either through the extension of their recorded ranges into México from Guatemala or by the recognition of species unknown in 1948, whereas some nominal species have been synonymized. *Microbatrachylus* has been regarded as synonymous with *Eleutherodactylus* (Lynch, 1965); four species of *Microbatrachylus* currently are regarded as valid (Duellman, 1961, Lynch, 1965). *Syrrhophus* was revised in part by Duellman (1958) and Firschein (1954), and a species of *Tomodactylus* transferred to *Syrrhophus* by Dixon (1957), who redefined *Tomodactylus* and added more species to the genus.

Since beginning my studies of the Mexican leptodactylids in 1962, I have become acutely aware of difficulties involved in defining the genera. A revision of *Eleutherodactylus* and a review of *Syrrhophus* are nearing completion, but prior to their publication it is desirable to redefine the genera of the Mexican leptodactylids, and in so doing recognize an heretofore unnamed genus. The definitions of *Eleutherodactylus* and *Leptodactylus* may need to be altered in the future, since both are widespread in South America and occur in the West Indies. Their definitions as given here are as precise as present knowledge permits. *Syrrhophus* and *Tomodactylus* are small assemblages that occur only in southwestern United States, México, and Guatemala.

Taylor (1952) synonymized *Engystomops* with *Eupemphix* which, although related, should be regarded as generically distinct (Gallardo, 1965). Perhaps the most conservative classification is that of Myers (1962) who, without published evidence, combined *Eleu-*

therodactylus, Syrrhophus, and the South American *Lithodytes* in a single genus.

The major problem for students working with the Mexican leptodactylids has not been the separation of *Engystomops* or *Leptodactylus* from other genera but the separation and definition of the eleutherodactyline frogs currently placed in three genera, *Eleutherodactylus, Syrrhophus,* and *Tomodactylus.* As will be shown in this paper, these are more conveniently placed in four genera. Once a fourth genus is recognized, certain phylogenetic problems disappear and a reasonable zoogeographic interpretation is possible for Middle American leptodactylid distribution.

ANALYSIS OF CHARACTERS

In México and northern Central America approximately 55 species of eleutherodactyline frogs (*Eleutherodactylus, Syrrhophus,* and *Tomodactylus*) are known. Four genera can be recognized on the basis of the nature of inguinal glands, morphology of the hands and feet, and certain osteological features.

Glands

Leptodactylids have a variety of glands that have been used as generic characters. Smith and Taylor (1948) regarded the so-called inguinal gland as a generic character in Mexican eleutherodaycty-lines. Lynch (1965) showed that *Eleutherodactylus* and *Micro-*

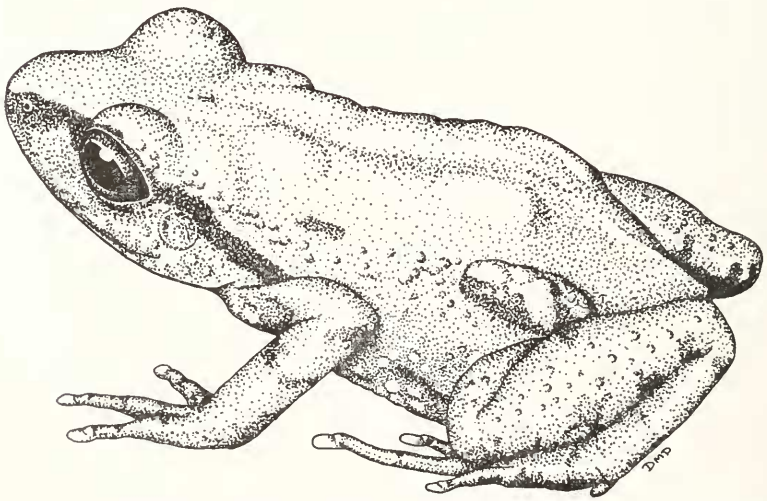

Fig. 1. *Tomodactylus angustidigitorum* (UMMZ 114305, × 4.5) illustrating the lumbo-inguinal gland typical of members of the genus. From a kodachrome by Wm. E. Duellman.

batrachylus cannot be separated by the nature of the gland or the condition of the prevomers (dentate or not). *Syrrhophus* and *Tomodactylus,* as defined by Smith and Taylor (1948), are not generically distinct because of overlap in the condition of the prevomers and in the development of the gland. Firschein (1954) stated that *Syrrhophus* differed from *Tomodactylus* by having an axillary gland, but it is now known that one species of *Syrrhophus* lacks the gland.

The inguinal glands of *Eleutherodactylus* and *Syrrhophus,* if present, are diffuse, irregular in outline, and generally not prominent; in *Tomodactylus* the gland is higher on the body (a lumbo-inguinal gland), compact, oval in outline, and prominent (Fig. 1). Axillary glands occur in most *Syrrhophus* but are not know in *Tomodactylus* or *Eleutherodactylus.*

Hands and feet

The tips of the digits are laterally expanded in most *Eleutherodactylus, Syrrhophus,* and *Tomodactylus.* Two species of *Eleutherodactylus* (*augusti* and *tarahumarensis*) and two *Tomodactylus* (*angustidigitorum* and *grandis*) lack any expansion of the digital tips. All but two of the species of eleutherodactyline frogs (*E. augusti* and *E. tarahumarensis*) have a transverse groove across the tips of the digits (Fig. 2).

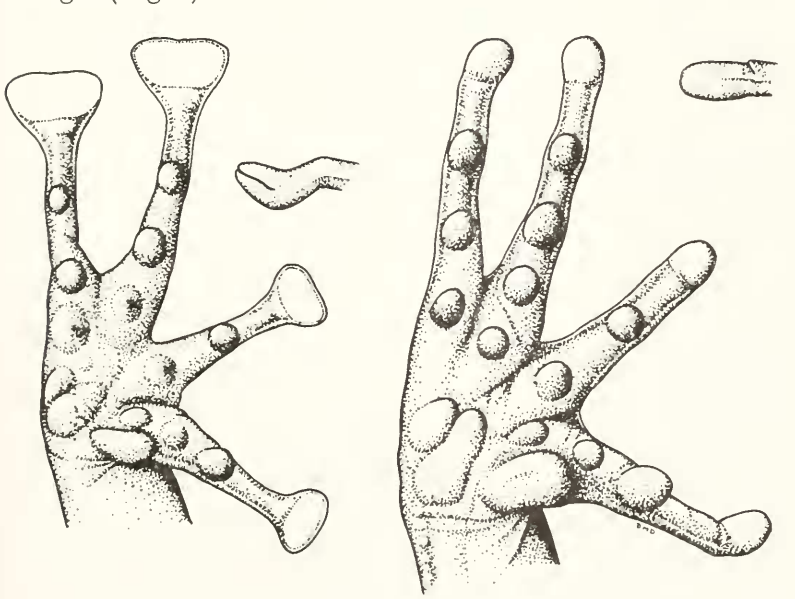

FIG. 2. Palmar views of the hands and lateral views of the tip of the third digits of *Eleutherodactylus alfredi* (left, KU 93994, × 5) and *Hylactophryne augusti* (right, KU 102594, × 3.

Supernumerary tubercles rarely are present on the feet of *Eleutherodactylus,* but are present and numerous in every species of *Syrrhophus, Tomodactylus,* and in the members of the *augusti* group of *Eleutherodactylus* (Fig. 3). The tubercles are small and numer-

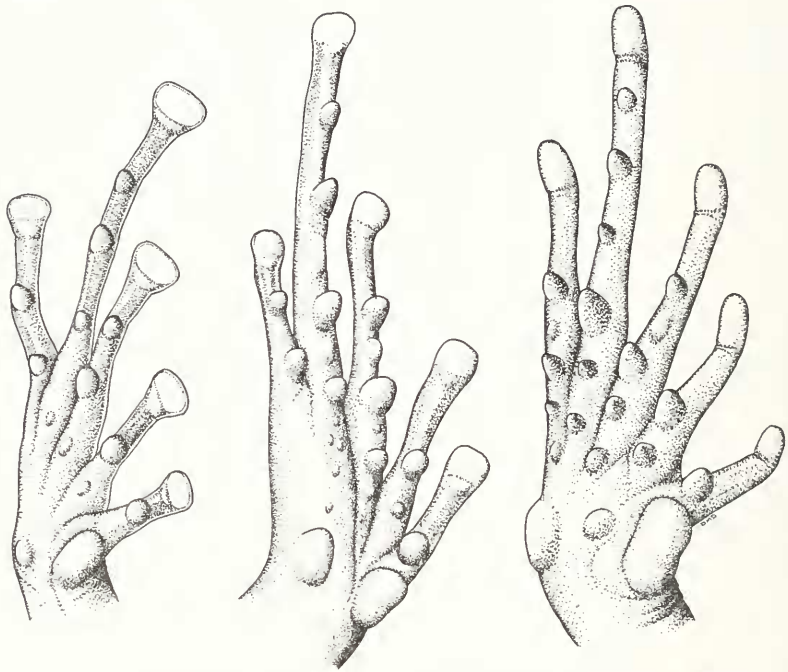

Fig. 3. Plantar views of feet of *Eleutherodactylus alfredi* (left, KU 93994, × 4.5), *Syrrhophus pipilans nebulosus* (middle, KU 58900, × 7.5), and *Hylactophryne augusti* (right, KU 102594, × 3) showing differences in size and arrangement of supernumerary tubercles.

ous in *Syrrhophus* and larger in *Tomodactylus* and the *Eleutherodactylus augusti* group. Most species of *Eleutherodactylus* have no plantar supernumerary tubercles; a few species have such tubercles, which never extend between the metatarsal tubercles as in *Syrrhophus* and *Tomodactylus.*

Tarsal folds and tubercles are lacking in *Syrrhophus, Tomodactylus,* and the *augusti* group of *Eleutherodactylus.* Several species of *Eleutherodactylus* lack tarsal folds and tubercles, but in nearly every species group, one or more species possess either an inner tarsal fold, inner tarsal tubercle(s), or outer tarsal tubercles.

The terminal phalanges of *Syrrhophus, Tomodactylus,* and all *Eleutherodactylus* (except the frogs of the *augusti* group) are dis-

tinctly T-shaped. In the latter, the bones are knob-shaped distally (Fig. 4). T-shaped terminal phalanges also are present in *Lithodytes* and *Trachyphrynus* but not in other leptodactylid genera. At least one species of *Eupsophus* (*E. quixensis*) has terminal phalanges that resemble those of the *Eleutherodactylus augusti* group.

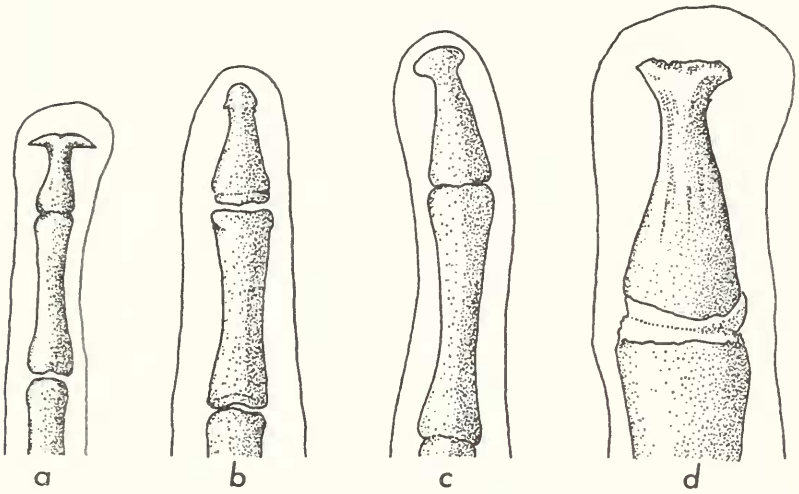

Fig. 4. Terminal phalanges of four leptodactylid frogs (all × 13.5). (a) *Eleutherodactylus mexicanus*, KU 55593; (b) *Eupsophus roseus*, KU 84731; (c) *Eupsophus quixensis*, UIMNH 59643; and (d) *Hylactophryne augusti*, KU 56192.

Several species of *Eleutherodactylus*, *Syrrhophus*, and *Tomodactylus* with slender fingers have T-shaped terminal phalanges although the terminal dilations proportionately are only scarcely wider than the finger tips in the *Eleutherodactylus augusti* group. The presence of a terminal groove at the tip of the finger is an external indicator of the T-shaped terminal phalanges.

Skull

All Mexican eleutherodactyline frogs have quadratojugal-maxillary articulations, compeltely roofed skulls in adults, median contact of the nasals, separated occipital condyles, and large prevomers. The premaxillae of all species are visible when the skulls are viewed from directly above. The pterygoid lacks a medioventral flange and does not meet the palatine. In no species is the anterior arm of the squamosal in contact with the maxillary. Of the numerous species examined (30 *Eleutherodactylus*, four *Syrrhophus*, and four *Tomodactylus*), the species in the *Eleutherodactylus augusti* group are unique in having a sphenethmoid with a blunt anterior edge.

Pectoral Girdle

All species have large cartilaginous plates in the pectoral girdles; none possesses a bony style. No divergent modifications of the clavicle and coracoid bones are known in the family.

GENERIC ACCOUNTS

Genus **Eleutherodactylus** Dumeril and Bibron, 1841

Type-species.—*Hylodes martinicensis* Tschudi, 1838

Diagnosis and definition.—Small to large frogs (12 to 110 mm. snout-vent length) having slightly to widely expanded digital pads, each pad bearing a terminal transverse groove; lumbo-inguinal, inguinal, and axillary glands absent, or if present, diffuse, irregular in outline, not compact; plantar supernumerary tubercles absent, or if present, six or fewer, restricted to distal area of plantar surface, and not extending between metatarsal tubercles; tarsus bearing inner or outer tubercles or folds or not; toes free to one-half webbed; terminal phalanges T-shaped; sternum cartilaginous, lacking bony style; sphenethmoid not truncate anteriorly; nasals in contact medially; maxillary and quadratojugal in contact; anterior arm of squamosal not in contact with maxillary; dermal cranial elements not involved in integumentary-cranial co-ossification; prevomers large, dentigerous processes present or not, dentate or not; maxillary and premaxillary bones dentate; occipital condyles separated; development direct.

Composition.—About 420 names have been applied to frogs of this genus; many of these names are synonyms, and many other species remain undescribed and unnamed. Perhaps the genus contains 350 species. Thirty-one species occur in México and northern Central America.

Distribution.—From Tamaulipas and Sinaloa, México, exclusive of the Mexican Plateau, to at least Peru and southernmost Brazil and throughout the West Indies. Introduced into Florida.

Etymology.—Greek (*eleuthero* + *dactylus*) meaning free-toed.

Genus **Engystomops** Jiménez de la Espada, 1872

Type species.—*Engystomops petersi* Jiménez de la Espada, 1872

Diagnosis and definition.—Small frogs (20 to 40 mm. snout-vent length) having undilated digital tips lacking transverse grooves; lumbo-inguinal or inguinal glands absent; plantar supernumerary tubercles present, extending between metatarsal tubercles; tarsus bearing spinelike tubercle on inner edge; toes free; terminal phalanges pointed; sternum bearing bony style; spenethmoid not truncate anteriorly; nasals in contact medially; maxillary and quadratojugal in articular contact; anterior arm of squamosal not in contact with maxillary; dermal cranial elements not involved in integumentary-cranial co-ossification; prevomers moderate in size, lacking teeth; maxillary and premaxillary bones edentate; occipital condyles separated; tadpole free living.

Composition.—Four nominal species (*E. petersi, E. pustulatus, E. pustulosus* and *E. schereri*).

Distribution.—Central Veracruz and eastern Oaxaca, México, to Trinidad, Bolivia, and Peru, east of the Andes.

Etymology.—*Greek* (*engys* + *stoma*) meaning narrow-mouthed.

Genus **Hylactophryne** new genus

Type-species.—*Hylodes augusti* Dugés, 1879

Diagnosis and definition.—Medium to large frogs (37 to 94 mm. snout-vent length) having undilated digital tips lacking terminal grooves; lumbo-inguinal or inguinal glands absent; plantar supernumerary tubercles present, prominent, extending to but not between metatarsal tubercles; tarsus lacking tubercles or folds; toes free of webbing; terminal phalanges knob-shaped, lacking elongate lateral expansions; sternum cartilaginous, lacking bony style; sphenethmoid truncate anteriorly; nasals in contact medially; maxillary and quadratojugal in articular contact; anterior arm of squamosal not in contact with maxillary; dermal cranial elements not involved in integumentary-cranial co-ossification; prevomers large, bearing dentigerous processes; maxillary and premaxillary bones dentate; occipital condyles separated; development direct.

Composition.—Two species, *H. augusti* and *H. tarahumarensis,* the former composed of four subspecies (Zweifel, 1956).

Distribution.—From Arizona, New Mexico, and Texas to Guerrero and Puebla, México, and a relict population on Cerro Quingola (just west of the Isthmus of Tehuantepec, México).

Etymology.—Greek (*hylactor* + *phryne*) meaning barking toad; in reference to the voice and common name.

Genus **Leptodactylus** Fitzinger, 1826

Type-species.—*Leptodactylus typhonia* Fitzinger, 1826

Diagnosis and definition.—Small to large frogs (30 to about 200 m.. snout-vent length) having undilated to slightly expanded digital tips bearing pads, no transverse groove at tips of digits; lumbo-inguinal, axillary, and/or ventral glands present or not, low, diffuse; plantar supernumerary tubercles generally absent, if present not extending between metatarsal tubercles; tarsus bearing tarsal folds or not; toes free of webbing, extensive lateral fringes present in some species; terminal phalanges pointed, not T-shaped; sternum bearing bony style; sphenethmoid not truncate anteriorly; nasals in contact medially; maxillary and quadratojugal in articular contact; anterior arm of squamosal not in contact with maxillary; dermal cranial elements not involved in integumentary-cranial co-ossification; prevomers large, bearing dentigerous processes; maxillary and premaxillary bones dentate; occipital condyles separated; tadpole free living.

Composition.—Sixty species according to Smith and Taylor (1948); 54 according to Gorham (1963); Argentianian authors have described several more in recent years.

Distribution.—Southern Sonora, México, and southern Texas throughout the Central and South American lowlands to Argentina. Also known from Hispaniola and Puerto Rico in the Greater Antilles and a few islands in the Lesser Antilles.

Entymology.—Greek (*leptos* + *dactylus*) meaning slender toes.

Genus Syrrhophus Cope, 1878

Type-species.—*Syrrhophus marnockii* Cope, 1878

Diagnosis and definition.—Small to medium sized frogs (18 to 40 mm. snout-vent) having slight to prominent digital expansions with transverse groove at tip of each digit; lumbo-inguinal and inguinal gland flattened, irregular in outline, not compact and oval; axillary glands present or not; plantar supernumerary tubercles numerous, more than eight, usually extending between metatarsal tubercles; tarsus lacking tubercles or folds; toes free or basally webbed; terminal phalanges T-shaped; sternum cartilaginous, lacking bony style; sphenethmoid not truncate anteriorly; nasals in contact medially; maxillary and quadratojugal in articular contact; anterior arm of squamosal not in contact with maxillary; dermal cranial elements not involved in integumentary-cranial co-ossification; prevomers large, usually lacking dentigerous processes and teeth; maxillary and premaxillary bones dentate; occipital condyles separated; development direct.

Composition.—Thirteen species; the species described as, or later referred to, *Syrrhophus* from Lower Central America and South America are *Eleutherodactylus* or *Eupsophus.*

Distribution.—Low to moderate elevations from Sinaloa, México, to Guatemala on the Pacific versant; from the Edwards and Stockton plateaus of Texas to British Honduras on the Caribbean versant.

Etymology.—Greek, emendation of *syrrhaptos,* meaning sewn together in reference to the united outer metatarsals.

Genus Tomodactylus Günther, 1900

Type-species.—*Tomodactylus amulae* Günther, 1900.

Diagnosis and definition.—Small frogs (20 to 35 mm. snout-vent length) having digital expansions or not, with transverse groove across tip of each digit; lumbo-inguinal gland prominently elevated, compact, oval, often patterned; axillary glands absent; plantar supernumerary tubercles numerous, more than eight, usually extending between metatarsal tubercles; tarsus lacking tubercles or folds; toes free; terminal phalanges T-shaped; sternum cartilaginous, lacking bony style; sphenethmoid not truncate anteriorly; nasals in contact medially; maxillary and quadratojugal in articular contact; anterior arm of squamosal not in contact with maxillary; dermal cranial elements not involved in integumentary-cranial co-ossification; prevomers large, usually bearing dentigerous processes; maxillary and premaxillary bones dentate; occipital condyles separated; development direct.

Composition.—Ten species.

Distribution.—The southern edge of the Mexican Plateau from Sinaloa to Veracruuz and onto the Oaxaca highlands and Sierra Madre del Sur.

Etymology.—Greek (*tomis* + *dactylus*) meaning knife toe; in reference to either the sharp subarticular tubercles or the unwebbed toes.

DISCUSSION

The preceding definitions only slightly alter the present generic limits of Mexican leptodactylids. Two species, previously regarded as *Eleutherodactylus,* are transferred to the new genus *Hylacto-*

phryne. The arrangement of the species of *Syrrhophus* and *Tomodactylus* remains the same as concluded by Dixon (1957), Duellman (1958), and Firschein (1954) in their reviews of the genera.

Lumbo-inguinal glands are most prominent in the genera *Pleurodema* and *Tomodactylus.* Various nondescript glands are present in many genera, but none is so well developed as those of *Pleurodema* and *Tomodactylus.*

At least nine leptodactylid genera are either known or thought to be terrestrial breeders lacking a free-living tadpole stage (*Eleutherodactylus, Euparkerella, Hylactophryne, Niceforonia, Noblella, Sminthillus, Syrrhophus, Tomodactylus* and *Trachyphrynus*). *Niceforonia* and *Trachyphrynus,* and probably *Hylactophryne,* are not closely related to the other genera. Direct development probably is an adaptation to adverse environmental conditions since many of the species occur in semi-arid or cold (Andean páramos) areas. *Eleutherodactylus* is generally thought to be the stock from which *Euparkerella, Noblella,* and *Sminthillus* evolved (Griffiths, 1959) and from which *Syrrhophus* and *Tomodactylus* are derived (Firschein, 1954).

The present distribution of *Hylactophryne* (isolated on the Mexican Plateau) and its digital form (like that of Papuan and many primitive South American leptodactylids) suggest that the genus was isolated in México throughout the Tertiary, whereas the other Central American genera are either post-Pliocene derivatives of *Eleutherodactylus* or invaders of Central America from South America since the mid-Pliocene land bridge was formed (Lloyd, 1963).

Piatt (1934) presented arguments against assigning *Eleutherodactylus latrans* to the genus *Lithodytes* and concluded that it was a "true" *Eleutherodactylus.* Contrary to his arguments, *latrans* (= *augusti* of Zweifel) and *E. tarahumarensis* Taylor differ from all other *Eleutherodactylus* (and *Syrrhophus* and *Tomodactylus*) in the nature of the tips of the digits (external and skeletal). The digits of *Hylactophryne* are like those of *Eupsophus.* My study of nearly all genera of leptodactylids indicates that Noble (1925) was correct in suggesting that *Borborocoetes* (= *Eupsophus*) is a close relative of *Eleutherodactylus latrans,* although Noble's arguments were based in part upon false evidence concerning the breeding habits of *E. latrans,* then thought to have a free-living tadpole.

Kellogg (1932) and Piatt (1934) argued that the terminal phalanges of *E. latrans* were typically eleutherodactyline. The variation of this character in *Eupsophus* (see Fig. 4) ranges from knobbed to bifurcate or Y-shaped (T-shaped in *Eleutherodactylus,*

Syrrhophus and *Tomodactylus*) and encompasses the nature of the character represented in *Hylatophryne*. *Eupsophus* differs from *Hylatophryne* in possessing a frontoparietal fontanelle, in generally having a maxillary-quadratojugal gap, and in having a free swimming tadpole stage.

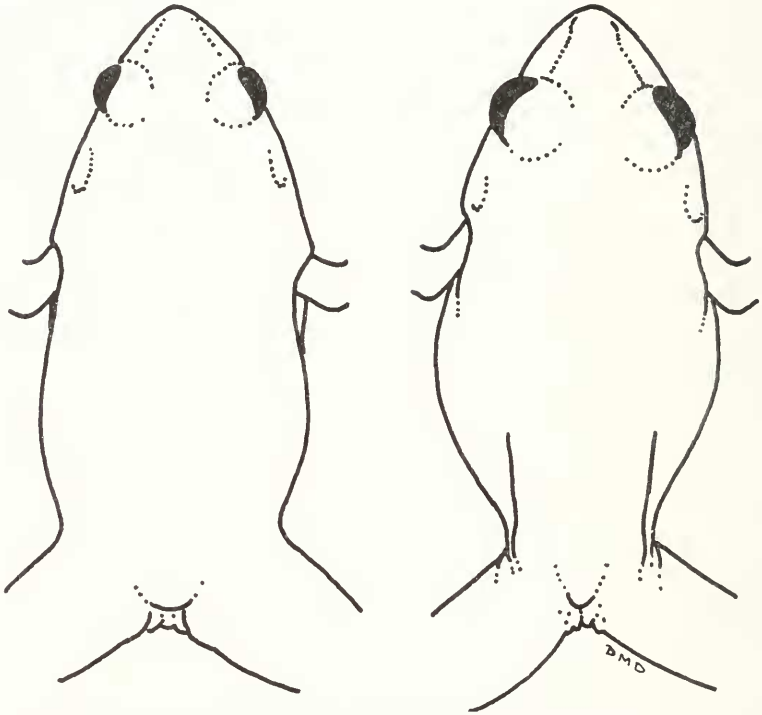

FIG. 5. Outline drawings of *Leptodactylus melanonotus* (left, KU 65704, × 2) and *Eleutherodactylus alfredi* (right, KU 93994, × 2).

KEY TO MEXICAN LEPTODACTYLID GENERA

1. Small (20-40 mm.), pustular, toadlike frogs; maxillary and premaxillary bones not bearing teeth ..... *Engystomops*
   Large (20-110 mm.), smooth skinned and non-toadlike frogs; maxillary and premaxillary bones bearing teeth 2
2. No conspicuous waist (Fig. 5); sternum bearing bony style, *Leptodactylus*
   Constrictions at waist (Fig. 5); sternum cartilaginous, no bony style .. 3
3. Few (less than six), if any, supernumerary tubercles on plantar surface ..... *Eleutherodactylus*
   Many (more than 8) supernumerary tubercles on plantar surfaces 4
4. Terminal, transverse groove across tip of digits, especially outer two fingers, digits expanded or not; small frogs (18 to 40 mm.) 5
   Tips of digits lacking transverse groove; digits unexpanded; medium-sized to large frogs (37 to 94 mm.) ..... *Hylactophryne*
5. Lumbo-inguinal gland compact, oval ..... *Tomodactylus*
   Lumbo-inguinal or inguinal gland absent or diffuse and irregular in outline ..... *Syrrhophus*

LITERATURE CITED

Dixon, J. R.
1957. Geographic variation and distribution of the genus *Tomodactylus* in Mexico. Texas Jour. Sci., 9:379-409, December.

Duellman, W. E.
1958. A review of the frogs of the genus Syrrhophus in western Mexico. Occas. Papers Mus. Zool. Univ. Michigan, 594:1-15, June 6.
1961. The amphibians and reptiles of Michoacan, Mexico. Univ. Kansas Publ. Mus. Nat. Hist., 15:1-148, December 20.

Firschein, I. L.
1954. Definition of some little understood members of the leptodactylid genus *Syrrhophus*, with a description of a new species. Copeia, 1:48-58, February 19.

Gallardo, J. M.
1965. A proposito de los Leptodactylidae (Amphibia Anura). Papeis Avulsos, 17:77-87, January 30.

Gorham, S. W.
1963. The comparative number of species of amphibians in Canada and other countries. III. Summary of species of anurans. Canadian Field-Nat., 77:13-48, March.

Griffiths, I.
1959. The phylogeny of Sminthillus limbatus and the status of the Brachycephalidae (Amphibia Salientia). Proc. Zool. Soc. London, 132:457-87, May.

Kellogg, R.
1932. Mexican tailless amphibians in the United States National Museum. Bull. U. S. Natl. Mus., 160:224 pp., March 31.

Lloyd, J. J.
1963. Tectonic history of the south Central-American orogen, *in* Childs and Beebe eds., Backbone of the Americas. Amer. Assoc. Petroleum Geol., pp. 88-100.

Lynch, J. D.
1965. A review of the eleutherodactylid frog genus *Microbatrachylus* (Leptodactylidae). Nat. Hist. Misc., 182:1-12, December 15.

Myers, G. S.
1962. The American leptodactylid frog genus *Eleutherodactylus, Hylodes* (= *Elosia*), and *Caudiverbera* (= *Calytocephalus*). Copeia, 1:195-202, April 11.

Noble, G. K.
1925. An outline of the relation of the ontogeny to phylogeny within the Amphibia. I. Amer. Mus. Nov., 165:1-17, April 16.

Piatt, J.
1934. The systematic status of Eleutherodactylus latrans (Cope). Amer. Midl. Nat., 15:89-91, February 15.

Smith, H. M. and Taylor, E. H.
1948. An annotated checklist and key to the Amphibia of Mexico. Bull. U. S. Natl. Mus., 194:1-118. June 7.